

Light-, Sound-, and Ultrasound-Induced Cercal Movements in Flying Crickets

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ABSTRACT—In tethered flying crickets (*Gryllus bimaculatus*), the cerci are medially displaced so that they are held parallel to each other. When unequal illumination was given with a single light to the compound eyes, only the cercus ipsilateral to the light source showed a lateral bending in the yaw plane. The amplitude of this cercal movement was proportional to the position of the light source up to about 90° (just perpendicular to the compound eyes), and it increased when the head was immobilized. When low-frequency sounds (0.5–15 kHz) were presented, the cercal movements occurred frequently in the cercus ipsilateral to the sound source. In contrast, in the presence of high-frequency sounds (20–30 kHz; ultrasounds) the cercal movements occurred predominantly in the contralateral cercus. When one of the forelegs bearing the tympanic organs was removed, the cercal movements occurred predominantly on the intact side and on the operated side in response to low- and high-frequency sounds, respectively.

INTRODUCTION

Most tethered crickets assume a straight and symmetrical flight posture with or without flapping their wings. In this flight posture, the fore- and midlegs are held close to the body, the abdomen is elevated, and the hindlegs are extended directly backward [18, 34]. The crickets assuming the flight posture show a head-rolling movement toward the light source and a co-ordinated rudder-like movement of the abdomen and legs in response to unequal illumination of the compound eyes [34]. Sound and ultrasound stimuli also elicit lateral swing of the antennae and a rudder-like movement of the abdomen and legs to one side [6, 12–15, 18, 20, 24]. Several insects exhibit these movements as specific maneuvers of flight, including locusts [1–3, 5, 26–28, 32], flies [10, 37], and dragonflies [17, 31].

In crickets, the movements of the head, legs, and abdomen elicited by external stimuli serve for steering during flight behavior [14, 34, 36]. Thus, a

head-rolling movement toward the light source and the co-ordinated rudder-like movement of the legs and abdomen result in orienting the dorsal surface toward the light source (dorsal light reaction) [34], while the yaw movement of the hindleg induced by sound and ultrasound contributes to steer the cricket toward the sound source (positive phonotaxis to calling songs) or away from it (negative phonotaxis to ultrasound) [11, 12].

We report here that, in addition to the head, leg and abdominal movements, flying crickets exhibit rudder-like bending movement of the cerci, a pair of abdominal appendages carrying sense organs sensitive to air movement and vibration, in response to light stimulation from various directions as well. Such a cercal movement could also be induced by directional acoustic stimulation depending on the sound frequency.

MATERIALS AND METHODS

Experimental animals

We used adult crickets (*Gryllus bimaculatus*) obtained from our laboratory colony in all experiments. The colony was maintained at a high density under controlled temperature conditions

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(26–28°C) with a 12:12 hr light-to-dark cycle.

Photographic analysis

To analyze in detail the cercal movements during tethered flight, photographs of the steering postures were taken with a 35-mm camera. The camera was placed at the ventral side of an animal. The animal was adhered by its pronotum to a steel rod (3 mm in diameter, 5 cm in length) with a mixture of beeswax and resin and attached to a supporting apparatus for unrestrained recording of flight posture. Most animals could begin flying or assuming the flight posture without flapping the wings as soon as their heads were exposed to a wind stream [34]. The angle between the body midline and longitudinal axis of the cercus was measured from the photographs.

Recording of cercal movements

Recordings of cercal movements were made using a capacitive position-sensing device developed by Sandeman [30] and Tomioka and Yamaguchi [34]. Briefly, sinusoidal signals of 40 kHz emitted from an oscillator were led to a fine wand of enamel-coated copper wire (50 μ m in diameter, 8 mm in length) attached with wax to each cercus along its longitudinal axis. Two pairs of metal ball sensors (6.5 mm in diameter), were arranged at either side of the fine wands at an equal distance. The sensors received the 40 kHz sinusoidal signals from the wands. For simultaneous recordings of both horizontal and vertical movements of the cercus, two pairs of sensors were arranged diagonally around the wand at an equal distance. The sinusoidal signals recorded by the two pairs of sensors were amplified by a two-channel differential amplifier, passed through a gate circuit and an RC filter and then recorded on a four-channel pen recorder with a light or acoustic stimulus monitor. To prevent the animal from removing the wands attached on the cerci during voluntary cleaning behavior with its hind legs, each tibia of the hind legs was cut off at the tibia-femur joint in advance. Although preliminary experiments showed no sex differences in cercal movements induced by light and acoustic stimulation, only males were used with light stimulation, since males had a tendency toward continuous flight

[34]. Only females were used with acoustic stimulation, since phonotaxis to calling song and ultrasound has been most thoroughly studied in females [e.g., 18, 20, 36].

Light and acoustic stimulation

A microlamp (Hamai Denkyu, 9V) controlled by a stimulator was used for illumination to the compound eyes. The position of the microlamp was manually changed using an apparatus which enabled the microlamp to move three-dimensionally around the animal with a distance of 3 cm from the animal. The intensity of the light stimulus was kept at 150 lx on the surface of the compound eyes. The acoustic stimuli used in this study were pure sine-wave tones generated by another oscillator through an envelope-shaping circuit and two kinds of speakers (Fostex FE 103 for frequencies up to 18 kHz; Onkyo TW-3001 for the higher frequencies from 18 to 30 kHz). The speakers were positioned just perpendicular to the longitudinal body axis at a distance of 10 cm from the animal. The sound stimuli of different frequencies were given to the animal at the same intensity. The sound pressure from the speakers was measured with a sound pressure measurement apparatus via a microphone (Brüel and Kjaer, 4135) to be from 70 to 80 dB at the position of the tethered animal. Sound frequencies higher than 30 kHz were not investigated.

RESULTS

Cercal movement induced by light stimulation

Most tethered crickets which assume flight postures with or without flapping their wings point their antennae straight ahead, hold the fore- and midlegs close to the body, and extend the abdomen and hindlegs directly backward. While the animal is assuming the flight postures, unequal illumination of the compound eyes induces not only a head-rolling movement toward the light source but also a bending movement of the abdomen and hindlegs on the stimulated side [34].

It was found that once the animal assumed the flight posture with or without flapping the wings in response to wind stimulation to the head, both

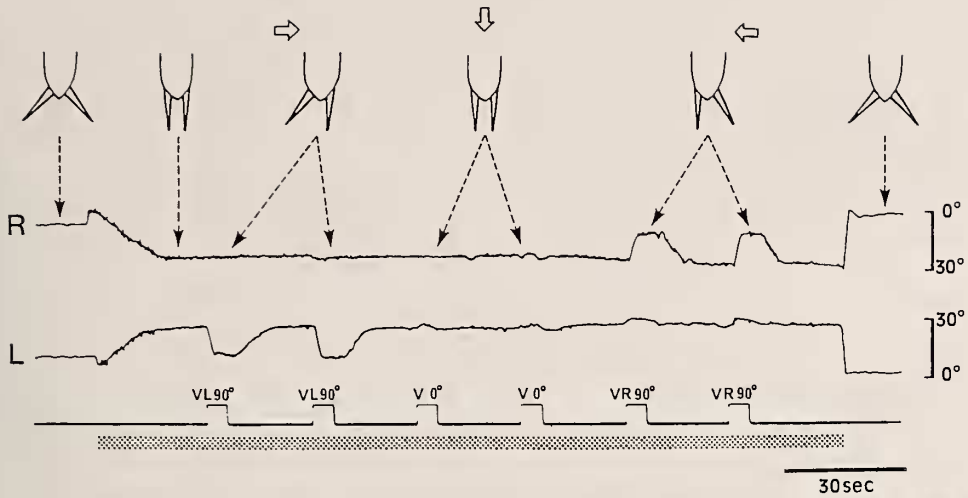


FIG. 1. Recordings of the light-induced cercal movements on both sides. Light stimuli were given from just lateral to the left eye ($VL90^\circ$), just above the head ($V0^\circ$) and just lateral to the right eye ($VR90^\circ$). The upward deflection in the first trace and the downward deflection in the second trace indicate the lateral bending in the right (R) and left (L) cerci. The third trace is the monitor of light stimulation (upward deflection, light on) and the dotted rectangle on the bottom indicates the period of flight. The schematic illustration on the top shows the position of cerci associated with flight and light stimulation. The open arrows indicate the direction of light stimuli.

cerci began to open for a while, followed by their gradual closing toward the midline until they became parallel to each other (Fig. 1). When the cerci were in such a position and the compound eyes were unequally illuminated by a single light, lateral bending mainly in the yaw plane was induced in the cercus ipsilateral to the light source (Fig. 1). No lateral bending was recorded in the contralateral cercus with such illumination. When the light source was positioned just above the head (equal illumination of the compound eyes), no obvious movement was induced in either cercus. The lateral bending of the cercus ceased quickly and both cerci returned to the original position, if the animal stopped flying, either voluntarily or involuntarily (for example, through contact with the tarsi), whether the wind persisted unchanged or not. At such a resting state, no movements were induced in the cerci by light stimulation. The amplitude of lateral bending of the cercus varied with the position of light source (Fig. 2): the amplitude became larger as the light source moved toward lateral in the horizontal plane. The cercal movement in response to light stimulation usually occurred in the horizontal plane. The cercal

movement in the pitching plane was barely recorded regardless of the position of light source, although the cerci were displaced slightly downward after the onset of flight.

As shown in Figure 3A,B, the cercal movement was barely induced when the light source was positioned from just above or under the head and just in front or behind the animal. However, when the light source was positioned between 0° (above) and 90° (lateral) in the vertical plane, only the cercus ipsilateral to the illuminated side bent laterally. The amplitude of this cercal movement was in proportion to the position of light source up to a maximum of 90° . It decreased gradually with the positional change of light source from 90° to 180° (under the head, Fig. 3A). The contralateral cercus maintained a steady position with an angle of about 5° regardless of the position of light source. A similar change of the cercal response to light was observed when the position of light source was changed in the horizontal plane (Fig. 3B). The maximum cercal angle was obtained with the light source positioned just lateral to the ipsilateral eye (90°).

To examine whether cercal movements were

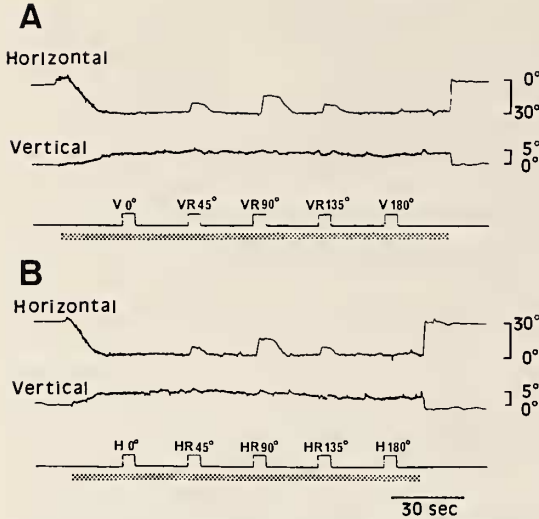


FIG. 2. Three dimensional recordings of the light-induced cercal movements on the right side. The light stimuli were given from various directions in the vertical plane (A) and horizontal plane (B). $V0^\circ$, just above the head; $VR45^\circ$, upper right; $VR90^\circ$, just lateral to the right eye; $VR135^\circ$, lower right; $V180^\circ$, just under the head. $H0^\circ$, just in front of the head; $HR45^\circ$, right frontal; $HR90^\circ$, just lateral to the right eye; $HR135^\circ$, right dorsal; $H180^\circ$, just behind the body. The first and second traces indicate the horizontal and vertical components of the cercal movement respectively. Upward deflection in the first trace and downward deflection in the second trace indicate the movements toward the stimulated side and the upward movements respectively. See Figure 1 legend for further explanation.

affected by proprioceptive feedback from the sensory hairs on the neck hair plate or visual feedback from the compound eyes, the head was fixed with wax to the prothorax. As shown in Figure 4, when the head was immobilized, the amplitude of cercal movement increased within the range of 40° to 120° light position in the horizontal plane. This result strongly suggests that the neck movement-related feedback plays an important role in the control of visually mediated cercal movements.

Cercal movement induced by acoustic stimulation

The cercal movements in the yaw plane were also induced by acoustic stimulation during flight. These movements had a close relation not only to the position of the sound source but also to its

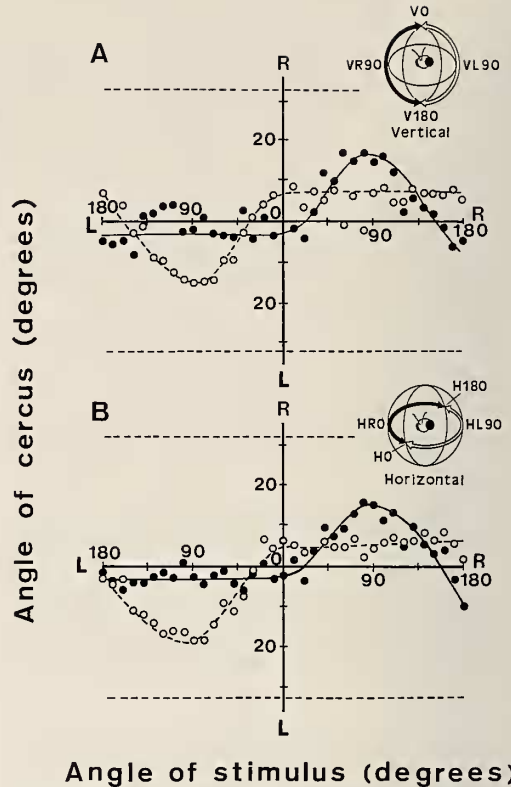


FIG. 3. Relation between the position of light stimulus and the angle of cercus. (A) The position of a microlamp was varied in the vertical plane (the angles of 0° , 90° , 180° in the abscissa correspond to the positions at just above the head, just lateral to the eye, and just under the animal respectively). R, right side; L, left side. (B) The position of the light source was varied in the horizontal plane (the angles of 0° , 90° and 180° in the abscissa correspond to the positions at just in front of the head, just lateral to the eye, and just at the back of the animal respectively). Open circles, left cercus; filled circles, right cercus. Both upper and lower broken lines in A and B indicate the angle of the cercus (about 33°) on both sides during rest.

frequency. As shown in Figure 5A, with low-frequency sounds of 0.5 to 15 kHz, cercal movements were recorded more frequently in the cercus ipsilateral to the sound source than in the contralateral cercus. By contrast, with high-frequency sounds (ultrasounds) of 20 to 30 kHz, the cercal movements were recorded more frequently in the contralateral cercus than in the ipsilateral one (Fig. 5B).

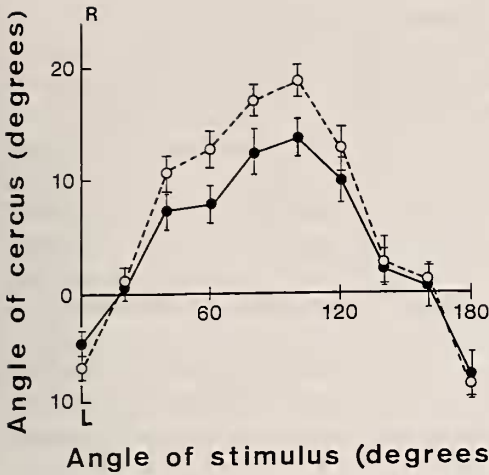


FIG. 4. Cercal response to visual stimulation before (solid line) and after (broken line) the fixation of the head. The position of a microlamp was changed in the horizontal plane and the angle of the right cercus was measured. Each point with a vertical bar indicate the mean of three measurements with standard deviation respectively. See Figure 3 legend for further explanation.

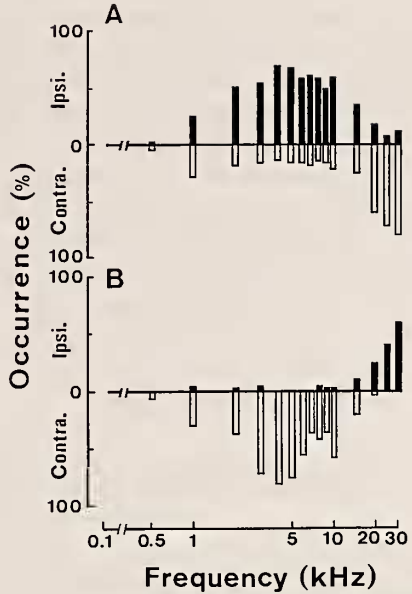


FIG. 6. Occurrence probabilities of cercal movements at various sound frequencies. (A) Intact animal (B) The tympanic organ ipsilateral to the sound source was removed. The occurrences are expressed as percentages of the number of total tests ($n=30$) at each frequency (ipsi., the cercal movements in the cercus ipsilateral to the sound source; contra., the cercal movements in the contralateral cercus).

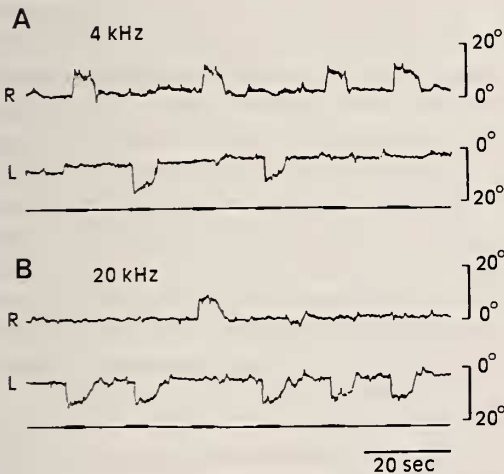


FIG. 5. Recordings of the cercal movements induced by acoustic stimuli of 4 kHz (A) and 20 kHz (B). In A and B, upward deflection in the first trace and downward deflection in the second trace indicate the movements in the right cercus (R) which is ipsilateral to the sound source and in the left cercus (L) contralateral to the sound source respectively. The third trace monitors the sound stimulation presented on the right side of the animal.

Figure 6A shows the percentages of the occurrence of cercal movements at each frequency when the cercus is ipsilateral and contralateral to the sound source, respectively: the bimodality which the cercus moves first in one direction and then the other at each frequency is indicated, though the direction of cercal movement basically depends on the sound frequency. It should be noted that the occurrence at each frequency did not reach a total 100% because of the failure of some cercal movements. No cercal movements in the pitching plane in either cercus were induced, irrespective of the position of the sound source and of the sound frequency.

In order to check the mutual interaction between auditory inputs from both sides, the tympanic organ on the stimulated side was eliminated by cutting off the foreleg on which the tympanic organ existed at its trochanter-femur joint (Fig. 6B). When the sounds of 0.5 to 15 kHz were presented, the cercal movements were more frequent on the

intact side than on the operated side, i.e., the stimulated side. With ultrasounds of 20 to 30 kHz, the cercal movements occurred predominantly in the cercus ipsilateral to the sound source. Therefore, it is evident that after removing one tympanic organ, the relation between the position of the sound source and the predominantly responsive cercus was reversed for all the tested stimulus frequencies. The bimodality of cercal movements clearly observed in the intact animal was rarely detected in the operated animal. The failure of cercal movements somewhat increased at each frequency after removing the foreleg.

DISCUSSION

Functional significance of cercal responses to visual and acoustic stimuli in steering behavior

Flying tethered crickets exhibit a dorsal light reaction which turns their backs toward the center of overall illumination [34], a positive phonotaxis to low-frequency sounds, and a negative phonotaxis to high-frequency sounds (ultrasounds) [e.g., 7, 19–23, 35]. This behavioral orientation to stimulus sources is based on a variety of flight maneuvers such as the asymmetrical amplitude change of the wing beat and rudder-like movement of the hindlegs [11, 12]. The hindleg movement produces a change of air resistance to the windstream present around the body and thus enable the flying crickets to turn and direct their flight toward a stimulus source through an interaction with the hindwings. However, the rudder-like movement of the abdomen does not seem to contribute to yaw turns, although it occurs in response to ultrasound [11]. This suggests a possibility that ruddering of the cercus is also ineffective for orientation to the stimulus source because of its very small surface area and light weight. If it should have any effect on the cricket's flight path, it would probably be less direct than that of the hindlegs. In view of the multisegmental nature of steering behavior, the cercal movement in the yaw plane could be regarded as one component reflex associated with that behavior, although it does not seem to play a direct role in steering.

In support of this assumption, yawing move-

ments could be observed in the antennae during flight as well. The amplitude of the antenna yawing movements changed with the direction of light stimuli just as the cercal movements. In addition, during equal illumination of the compound eyes with a light source the fore- and midlegs are held tightly close to the body on both sides, but during unequal illumination the legs on the side ipsilateral to the light source slightly relax (Ohnishi and Yamaguchi, unpublished data).

The maintained displacement toward the midline has been also reported in the cerci of flying cockroaches [9]. No observation has yet been made on their cercal response to light and acoustic stimuli.

Sensory feedback control of the cercal response to visual stimulus

In the locust, the hairs on the neck plates play an important role in optomotor reactions. Sensory inputs from these hair plates compensate for the head-rolling angle [5]. In the present experiment, the amplitude of light-induced cercal movements was increased by fixing the animal's head to the ridge of the prothorax with wax (Fig. 4). Regarding the proprioceptive function of the sensory hairs, Tomioka and Yamaguchi [34] reported that no changes in the head-rolling angle were observed in the cricket whose sensory hairs on the hair plates were removed, waxed, burned out or controlled so as not to touch the prothoracic fringe. These facts suggest that the increase in response amplitude following the head fixation is probably due to the lack of feedback inputs from the visual system which would, under intact condition, delimit the response amplitude by decreasing aberration between the light source and the dorso-ventral axis of the head caused by the head rolling.

Effect of the direction and frequency of sound stimuli on the cercal response

The present experiment showed that the cercal movements in the yaw plane are induced by acoustic stimulation as well as by light stimulation. The most effective acoustic stimuli for producing the cercal movements were the sound of 4–5 kHz and the ultrasound of 30 kHz (the highest frequency used in the present experiment), corresponding to

such sounds as the conspecific calling song and ultrasounds emitted by bats, respectively. With the sounds of 0.5 to 15 kHz, the cercal movements were induced predominantly in the cercus ipsilateral to the sound source. With the ultrasounds of 20 to 30 kHz, they were induced mostly in the contralateral cercus (Fig. 6A). In this connection Moiseff *et al.* [18] reported that the flying crickets *Teleogryllus oceanicus* respond directionally to sound stimulation by bending their abdomens and hindlegs to one side: when they are stimulated with a model of a conspecific calling song with a carrier frequency of from 3 to 9 kHz, they turn toward the sound source, while they turn away from the same song pattern played at carrier frequencies from 30 to 70 kHz.

Concerning the directional response to acoustic stimulation, another point of interest was that the response was bimodal: the animal bents one cercus in some cases and the opposite one in other cases responding to acoustic stimuli of the same frequency (Fig. 6A). In addition, the occurrence of the cercal response to acoustic stimulation was not deterministic: the cercal responsiveness ranged from 10% to 90%, never reaching 100% at any frequency. Moiseff *et al.* [18] also reported the bimodality of abdomen yawing movements toward or away from the sound source and the failure of performing yawing movements in *Teleogryllus oceanicus*.

One possible explanation for the bimodality of cercal responses to acoustic stimulation is that the bimodality observed over a wide frequency range may result from the cricket's inaccurate ability to estimate the direction of the sound source, though the directional responsiveness of the cerci must be due to true frequency discrimination. Such errors in sound location do occur also in female crickets tracking the source of a male's calling song by auditory cues [8, 33]. A second possibility is that the bimodality of directional responses does not merely indicate the cricket's intent to steer toward low-frequency sounds and away from high-frequency sounds, but instead it, including the failure of cercal response, may result in unpredictable steering responses which should be adaptive since the predators such as bats have little chance of learning the insect's strategies [16, 29]. The

present experiment showed that the cercal response to acoustic stimulation was almost unimodal after removing one tympanic organ (Fig. 6B). It is therefore suggested that the auditory inputs from both tympanic organs are involved not only in determining the directional responsiveness of the cerci, but also in mediating the "unpredictable cercal response". We should expect a rather complex mechanism of the bimodal responsiveness to be tightly coupled to the neural circuitry controlling flight.

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